

Biomechanics of Torsion in the Human Mandible

DAVID J. DAEGLING^{1*} AND WILLIAM L. HYLANDER²

¹*Department of Anthropology, Yale University, New Haven, Connecticut 06520*

²*Department of Biological Anthropology and Anatomy, Duke University Medical Center, Durham, North Carolina 27710*

KEY WORDS: stress; strain; mandibular function

ABSTRACT Comparative investigations of mandibular function among primates have relied upon elementary structural models to estimate states of masticatory stress and strain. In these studies, mandibular corpus morphology is idealized as a homogeneous, isotropic symmetrical body of invariant geometry, and this morphological abstraction is used to infer relative levels of stress and strain in the jaw. In reality, none of the limiting conditions assumed by these models is satisfied; consequently, it is prudent to ask whether this "textbook" engineering approach is valid for the inference of biomechanical behavior.

In this study, the predictions of various geometric representations of the mandibular corpus are evaluated against strains recorded in a sample of human jaws loaded in torsion. Symmetrical geometrical models (including various "robusticity" shape indices), although convenient, are probably not consistently reliable for predicting the distribution of strains in the corpus. The experimental data suggest that variations in cortical thickness within sections play a significant role in determining the profile of relative strains. For comparative applications, characterization of the corpus as an asymmetrical hollow ellipse (i.e., with differing thickness of medial and lateral cortical plates) may provide a reasonable portrayal of relative strains. *Am J Phys Anthropol* 105:73-87, 1998. © 1998 Wiley-Liss, Inc.

The purpose of a biomechanical model is to estimate the effects of forces on a body with a sufficient degree of accuracy. What qualifies as "sufficient" in this context is dependent upon the hypothesis under consideration, but with respect to biological systems there is no doubt that the application of a mechanical model provides only an approximate picture of what actually occurs *in vivo*. Whether the model involves a few linear measurements or a three-dimensional finite element mesh, the objective is that as we apply these simplified representations to different specimens or across a comparative sample, the mechanical consequences of differing morphologies will be revealed.

The mandibular corpus presents a challenge for biomechanical modelling: it is materially anisotropic, structurally heteroge-

neous and geometrically irregular. Perusal of any introductory engineering textbook reveals that the presence of these conditions precludes the application of the most basic models to mechanical questions. Even so, the portrayal of the mandible as a bent or twisted member of uniform structure and material is frequently encountered in the literature (Hylander, 1979a,b, 1981, 1984, 1985, 1988; Smith, 1983; Bouvier, 1986a,b;

Presented at the 1996 Annual Meeting of The American Association of Physical Anthropologists.

Contract grant sponsor: National Science Foundation; contract grant numbers SBR-9307969 and SBR-9514213; Contract grant sponsor: National Institutes of Health; Contract grant number DE04531.

*Correspondence to: David J. Daegling, Department of Anthropology, Yale University, New Haven, CT 06520-8277. Fax: (203) 432-3669. E-mail: david.daegling@yale.edu

Received 6 November 1996; accepted 28 September 1997.

Daegling, 1989, 1992, 1993; Daegling and Grine, 1991; Ravosa, 1991; Cole, 1992; Schwartz and Conroy, 1996). Despite the oversimplifications involved, the use of these elementary models has helped to establish that masticatory loads and mandibular corpus morphology are functionally linked (Hylander, 1979a, 1988). That is, it appears that these models work, at least up to a point.

Recent work has indicated that, as expected, the application of simple beam models are inadequate for prediction of absolute stress and strain magnitudes. In fact, finite element analyses (Korioth et al., 1992) and experimental investigations (Daegling and Hylander, 1994a,b) indicate that along alveolar margins the beam models may fail to predict even relative strain magnitudes. The reliability of the elementary "textbook" models, therefore, is obviously limited. Among the more pessimistic assessments of these types of models is the statement that "[m]easurements of corpus dimensions (either direct measurements or calculated "mechanical" variables) may be an order of magnitude or more in error in estimating the mechanical features of the mandible" (Smith, 1983: 325).

One reason that the simpler models have yielded insight into mandibular function is that they can predict (for a given loading condition) the location of maximum strains in jaws of different size and shape, without actually specifying what these strains are quantitatively. In the comparative context, the actual numerical values of these strains are less important than knowledge of how these strains are distributed in a given individual (the *strain gradient*),¹ and whether under identical loading conditions strains are equivalent in different individuals or species (*relative strain magnitude*).

The pattern of inferred strain gradients or relative strain magnitudes is obviously dependent on the model chosen to represent corpus morphology. This is especially true

for the loading condition of torsion, which is an important source of masticatory stress among primates (Hylander, 1979a,b, 1988). A variety of models has been employed to evaluate the biomechanics of torsion in primate jaws, and since each of these is premised on different assumptions, it is unlikely that all can be valid.

This paper reviews the alternative geometrical representations of the mandibular corpus that have been proposed as models of corpus mechanical behavior. Based on strain gradients observed empirically across a comparative sample under controlled loading conditions, the efficacy of each model is qualitatively assessed. This empirical evaluation of theoretical models addresses the following question: given the morphological complexity of the mandible, can the elementary models vital for comparative research provide reliable information about strain distribution in the mandible? If so, which models are most appropriate?

MODELS OF TWISTED MANDIBLES

Unfortunately, the choice of a biomechanical model for comparative study depends on a compromise between two factors: convenience vs. accuracy. The more accurate models require greater investment in specimen measurement and computation for deriving relevant variables (e.g., Demes et al., 1984; Daegling, 1992). On the other hand, one or two linear measurements may suffice for the simplest models (e.g., Hylander, 1979a; Bouver, 1986a,b; Ravosa, 1991), but at the certain though as yet undocumented expense of accuracy.

The *polar moment of inertia* is often the variable of choice for estimating torsional resistance in long bones, and quantities derived from it have been used for the quantification of torsional strength in primate mandibles (Smith, 1983). It has been recognized by several investigators, however, that mandibular models based on this quantity are bound to give inaccurate results (Demes et al., 1984; Daegling and Grine, 1991; Schwartz and Conroy, 1996). This variable is misleading since it is based on an assumption of axial symmetry, a condition rarely observed in the primate mandibular corpus. Under a condition of axial symme-

¹In this paper, the strain gradient is loosely defined as the difference in peak shear strains at different locations of a corpus cross-section. Unless stated otherwise, we are not using the term to connote a quantitative measure of strain changes over linear or areal dimensions.

try (i.e., a circular cross-sectional shape), it is assumed that along the periosteal surface, no strain gradient is present at a given cross section.

The idea that cylindrical cross sections provide the optimal shape for countering torsional moments can be quantified as the so-called "robusticity" index so often used in studies of hominoid taxonomy (Freyer, 1974; Greenfield, 1979; Wolpoff, 1977; Chamberlain and Wood, 1985). In its basic form, this ratio of corpus breadth to height can be employed to reflect the degree to which different species approach this ideal condition (Smith, 1983; Daegling, 1989). Others have modified this into a "bending index" consisting of a ratio of perpendicular area moments of inertia (Daegling and Grine, 1991; Schwartz and Conroy, 1996), on the grounds that it is more mechanically meaningful than the "robusticity" index since it accounts for details of cortical bone distribution. However these shape indices are calculated, they do not by themselves provide information about relative strain magnitudes (i.e., differences in strength) between individuals or taxa. Because information on size is hidden within the index, it is impossible to tell whether a mandible is "overdesigned" or "underdesigned" with respect to the loads it experiences, despite the fact that its cross-sectional shape may be "optimal." For example, in comparison to anthropoid primates, galago mandibles are "robust" by the criterion of the index. The pitfalls of this concept of robusticity are further exemplified by considering *Gigantopithecus* mandibles: these corpora are not very different in the "robusticity" index from modern hominoids, yet most workers would agree these mandibles are impressive in their load-bearing capacity due to their large absolute dimensions. In other words, since the "robusticity" or "bending" indices do not incorporate size information in their computation, they only provide information on strain gradients of particular shapes. Thus, even qualitative assessment of differences in peak strains between specimens cannot be inferred by exclusive reference to such indices.

The most frequently encountered model for comparing torsional resistance is the *ellipse*. Elliptical models may take many

forms, and all are attractive due to the fact that the shape of corpus cross sections is easily approximated. When corpus width is used as a variable reflecting torsional resistance (Hylander, 1979a, 1988; Bouvier, 1986a,b; Ravosa, 1991), it is basically a solid elliptical model (or a hollow elliptical model with no variation in cortical thickness) that is being employed. Both solid and hollow ellipse models predict similar strain gradients in torsion: shear strains will be highest at the ends of the ellipse's minor axis (i.e., along the periosteal bony surfaces around midcorpus) and significantly lower along superior and inferior borders. Although these models are convenient, from a strictly morphological point of view they are suspect because the documentation of cortical bone distribution reveals that a solid or uniformly thick hollow ellipse model does not reliably reflect mechanical differences among hominoid mandibles (Daegling, 1989). Biknevicius and Ruff (1992) have since pointed out that by allowing for variable thickness in the cortical shell, much more consistent depictions of actual morphology may be obtained. They have correctly noted that an asymmetrical hollow ellipse model provides a more accurate approximation of cross-sectional geometry than does a symmetrical model that does not allow for differences in cortical thickness between medial and lateral sides.

Even asymmetrical ellipse models, however, impose a geometric regularity to corpus shape that is rarely observed in nature. An alternative model to account for thickness variation while removing this geometrical constraint is a *thin tube* model. This model predicts high strains along the thinnest region of cortical bone within a section regardless of its location within that section (i.e., the thinnest region of bone is not constrained to lie in a particular location, such as the minor axis of an ellipse). A quantity based on the thin tube has been used to compare torsional strength in primate mandibles (Demes et al., 1984; Daegling, 1992); this variable (Bredt's formula) considers both cross-sectional area encompassed by the tube and the thickness of its walls. Bredt's formula (K) is analogous to a section modulus used to infer strength in bending and is

reckoned in dimensionally equivalent units (e.g., mm³). It is calculated by the formula $K = 2At_{min}$, where A is the area enclosed by the median axis of the tube and t_{min} is the minimum thickness of the tube wall.

The presence of teeth within alveoli has led a number of workers to suggest that, for some purposes, the mandible should be modelled as a member with open sections (Hylander, 1979b; Smith, 1983; Daegling, 1989). In the case of torsion, the choice between closed- or open-section models has tremendous implications, since an open section possesses a fraction of the rigidity of a closed one (Frankel and Burstein, 1965, 1970). The maximum strains in an open section are expected in the thickest area of compact bone (Young, 1989), in sharp contrast to the predictions of competing models. Preliminary experimental investigations, however, suggest that the corpus is unlikely to behave as an open section (Daegling et al., 1992).

None of these models makes any allowance for biomechanically relevant variables such as material anisotropy, bone density or structural heterogeneity. Thus their ability to predict absolute strain magnitudes or a precisely defined strain gradient is at best suspect. They do, however, provide a potentially useful means of comparing relative strain magnitudes between different individuals or species.

MATERIALS AND METHODS

Bone strain from a sample of human mandibles (Table 1) was measured to examine the efficacy of the alternative structural models (ellipse, thin tube, open section) outlined above. The use of in vivo data for verifying model accuracy is inappropriate since load magnitude and type cannot be controlled. Instead, an in vitro approach is preferable because the predictions of competing models can be tested against one another under known loading conditions.

Five formalin-fixed human hemimandibles were bilaterally twisted about their long axes and resultant surface strains recorded from four locations on the basal postcanine corpus. Rosette strain gages (FRA-1-1L rectangular rosettes [stacked], 1 × 0.7 mm gage length, 4.5 mm diameter backing, Texas

TABLE 1. *Experimental sample*

Experiment	Sex	Age	Dental status
A	M	86	I1-P4, M3
B	M	81	I1-P4, M2
C	M	82	complete (M2)
D	F	85	C-M1, M3
E	F	77	C-P4, M3

Teeth listed under dental status are those present in the hemimandible. Italicized teeth indicate the site below which rosette gages were bonded to the corpus.

Measurements, College Station TX) were bonded to bone along periosteal surfaces at the lateral midcorpus (LM), lateral basal aspect (LB), medial midcorpus (MM) and medial basal aspect (MB) in approximately the same coronal plane (Fig. 1). Specimens were loaded 10 times, with each loading and unloading cycle of 5 s duration. Within each experiment, the twisting moment applied to the specimen was constant, although it varied between experiments from 5.28 to 5.65 Nm. Specimens were kept wet throughout procedures.

Specimens were restrained at the ramus, which was embedded in a caroplastic block. Basal and alveolar margins were freely suspended during experiments. Equal and opposite loads were applied through two 5 mm screw eyes extended bilaterally from the anterior corpus of each hemimandible (Fig. 2). To minimize the effects of stress concentrations created at the site of load application, strains were sampled from sections at least 25 mm from these sites. Potential strain disturbances also may exist near the site of specimen restraint; strains were sampled anywhere from 21 mm (experiment D) to at least 37 mm (all other experiments) from these sites in an effort to minimize these effects.² The peak maximum and minimum principal strains (ϵ_1 and ϵ_2), shear strain (γ), and direction of maximum princi-

²Strain "disturbances" from the idealized theoretical conditions of the alternative models discussed are unavoidably created in an experimental context. That is, at sites adjacent to specimen restraints and points of load application, the strain environment becomes sufficiently complex that it cannot be satisfactorily described by these models. St. Venant's Principle (Nash, 1972) holds that these models can describe mechanical behavior at sections well-removed from restraint and load application sites. For a given experiment, it is not known to what degree these disturbances impact on measured strains. It is, however, possible to infer that these effects have not produced egregious alterations in the strain environment by observing whether the direction of maximum principal strains conforms to theoretical expectations of the loading context.

pal strain (α) were determined from the raw strains recorded from each rosette, and these values were averaged over the 10 loading cycles.

Following experiments, specimens were sectioned through the plane that included the four rosette gages. Average cortical thickness deep to each gage was calculated by measuring minimum periosteal-endosteal dimensions at five locations spaced at approximately 1 mm intervals. Area properties of the corpus for use in calculation of Bredt's formula and the "bending index" were obtained by digitizing cortical bone contours in the plane of section. The superior border of sections was constrained to lie no higher than the height of the interradicular crest.

To proceed with a consideration of the utility of the alternative models discussed, it must first be established that there is a consistency to the observed strains across the five experiments. In the investigation of the effects of torsion, the variable of primary interest is the peak shear strain. If the distribution of shear strains follows no pattern across the sample, then either simplified structural models have no biological validity or the experimental protocol was not measuring the desired conditions. Thus the statistical treatment of the experimental data first addressed whether consistency of results was obtained. Two tests for consistency of pattern were employed. First, the peak shear strains were rank-ordered within specimens (by rosette position) and this ordering across experiments was evaluated by Kendall's coefficient of concordance. Second, a multivariate profile analysis (Rencher, 1985) was performed using the mean peak shear strains at each rosette as variables. The design of the contrasts is similar to a multivariate analysis of variance using repeated measures (Wilkinson, 1990).

RESULTS

Direction of the maximum principal strains at midcorpus in the five experiments is depicted in Figure 3. The orientation of these principal strains at roughly 45° to the corpus long axis and the reversal in orientation between lateral and lingual surfaces strongly suggest that the desired state of a "pure" torsional moment was suitably ap-

proximated. Theory of twisted members also predicts a principal strain ratio (ϵ_1/ϵ_2) of unity (1.0) in cylindrical specimens, yet in these experiments considerable departures from this predicted value were observed for locations other than the medial midcorpus (Table 2). Possible reasons for this discrepancy are addressed below (see Discussion), although it may be stated here that these apparently aberrant values do not contraindicate a loading condition of torsion, given that an "expected" ratio value is not known for specimens lacking regular geometry.

Despite individual morphological differences, the strain gradients observed under torsional loads are similar across the five experiments (Table 3). Highest strains are always found at midcorpus, and of these the strains along the medial surface exceed those along the lateral surface in every case. Strains along the basal corpus are consistently smaller relative to those at midcorpus. The rank-order of mean peak strains by rosette location is significantly consistent (Kendall's coefficient of concordance = 0.936, $P < .01$).

The profiles of the peak shear strains from individual experiments are illustrated in Figure 4, with the mean profile superimposed. It is necessary to know whether this mean profile is significant; that is, does this profile differ from a flat line? Put another way, are the means at the four rosette sites different from one another? This was assessed by a single sample profile analysis contrasting differences among pairs of means. Midcorpus rosette sites were not significantly different ($P = 0.062$) from one another, nor did the medial and lateral basal rosettes record significantly different shear strains ($P = 0.497$). Significant differences were demonstrated, however, between lateral midcorpus and lateral basal shear strains ($P = .006$), medial midcorpus and medial basal shear strains ($P = 0.016$), medial midcorpus and lateral basal strains ($P = 0.021$) and lateral midcorpus and medial basal strains ($P = 0.012$). From this analysis one concludes that midcorpus strains differ from basal corpus strains under a torsional loading regime.

Theoretical considerations suggest a relationship between peak shear strains and

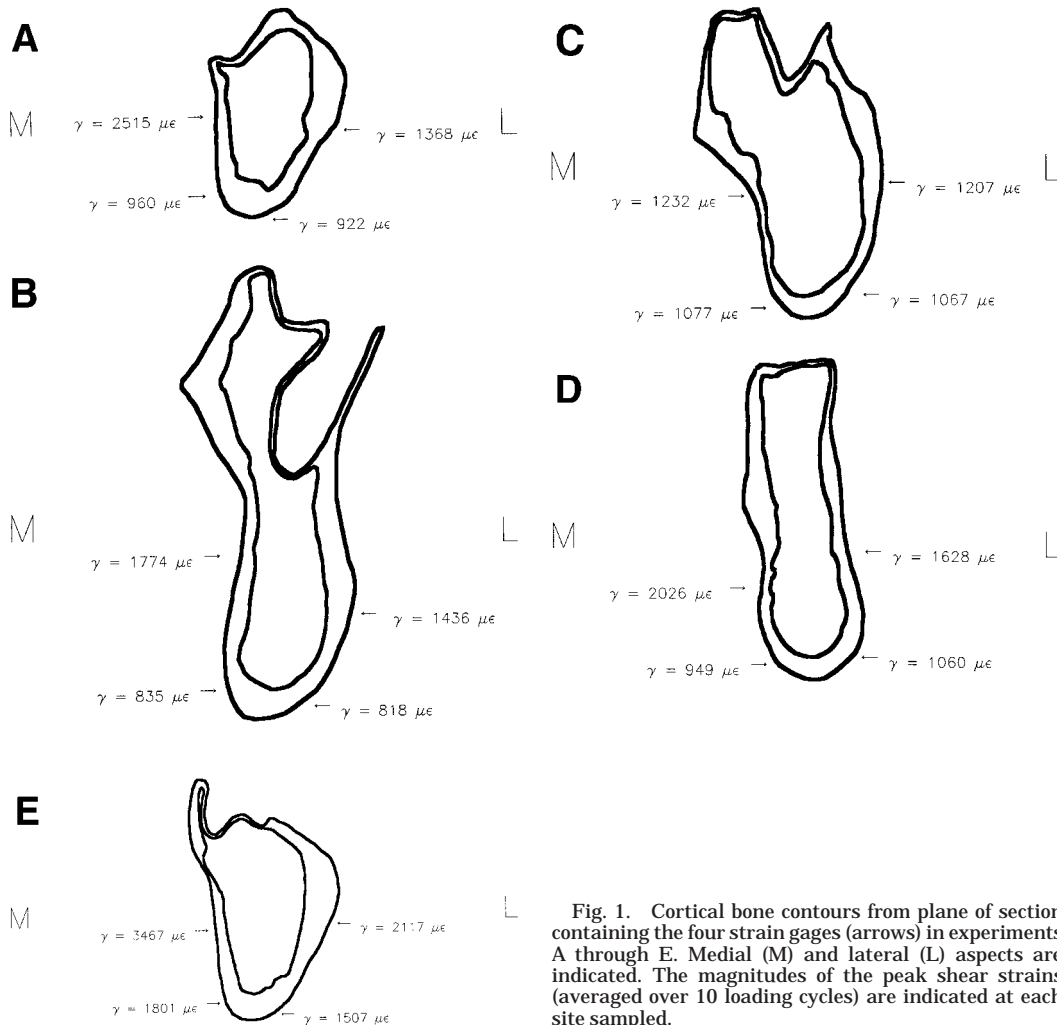


Fig. 1. Cortical bone contours from plane of section containing the four strain gages (arrows) in experiments A through E. Medial (M) and lateral (L) aspects are indicated. The magnitudes of the peak shear strains (averaged over 10 loading cycles) are indicated at each site sampled.

cortical thickness; specifically, the two variables should be negatively associated (except in the case of an open section). This would be borne out by examining their covariation both within and between specimens (Table 4), although statistical significance is only rarely observed in these comparisons. Given the relatively small number of individuals sampled ($N = 5$) and the limited sites sampled ($N = 4$), perhaps what is most surprising is that two contrasts are significant. These data suggest that local differences in cortical thickness have a predictable influence on shear strain magnitudes within a particular specimen, but that generalizing this relationship by a single linear model across individuals is inadvisable.

Ideally, what has been measured in these experiments are the effects of specimen size and shape on the one hand and those of rosette location on the other. Realistically, other factors are contributing to observed variance. These include variables of age, sex and dental status which have certain, but in the present study unknown effects on bone density and material anisotropy. The contribution of these factors to observed variation would ideally be assessed by a factorial ANOVA or equivalent design, but the distribution of these categorical variables and the limited number of specimens examined could not be expected to yield meaningful results. The impact of these factors on our results are consequently unestablished. Thus, generalizing these re-

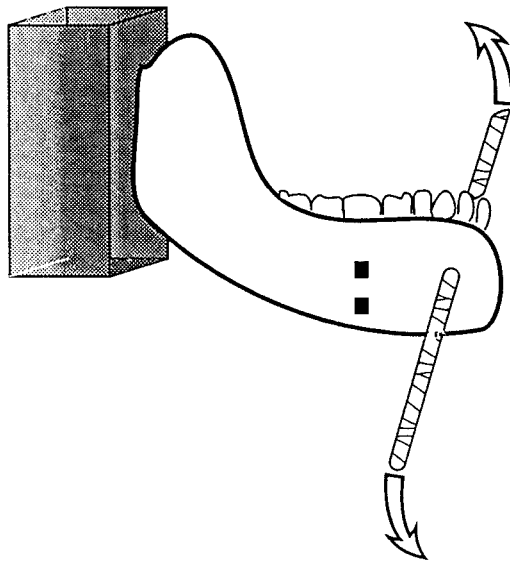


Fig. 2. Schematic illustration of experimental protocol. Specimens were restrained at the resin block in which the ramus was embedded. Loads were applied parallel to the gravity vector in opposite directions at points equidistant from lateral and medial periosteal surfaces. This loading condition was designed to insure that a torsional loading regime was primarily responsible for the strains observed. This twisting moment produced eversion of the alveolar process and inversion of the basal corpus. Loads were applied for 5 s duration and unloaded for 5 s over 10 cycles in each experiment. Location of strain gages on the lateral corpus is shown.

sults across human and nonhuman primate populations should be made with caution.³

DISCUSSION

Model predictions

The presence of consistent strain gradients among the sampled sites allows for an evaluation of alternative structural models. Two factors appear to account for the occurrence of relatively high shear strains: location near midcorpus and the presence of relatively thin cortical bone (Fig. 1). The fact that strains are consistently higher at midcorpus than along the basal aspect supports an ellipse model, although the difference

between medial and lateral midcorpus strains approaches statistical significance, which appears at odds with predictions for a symmetrical ellipse. If the endosteal borders

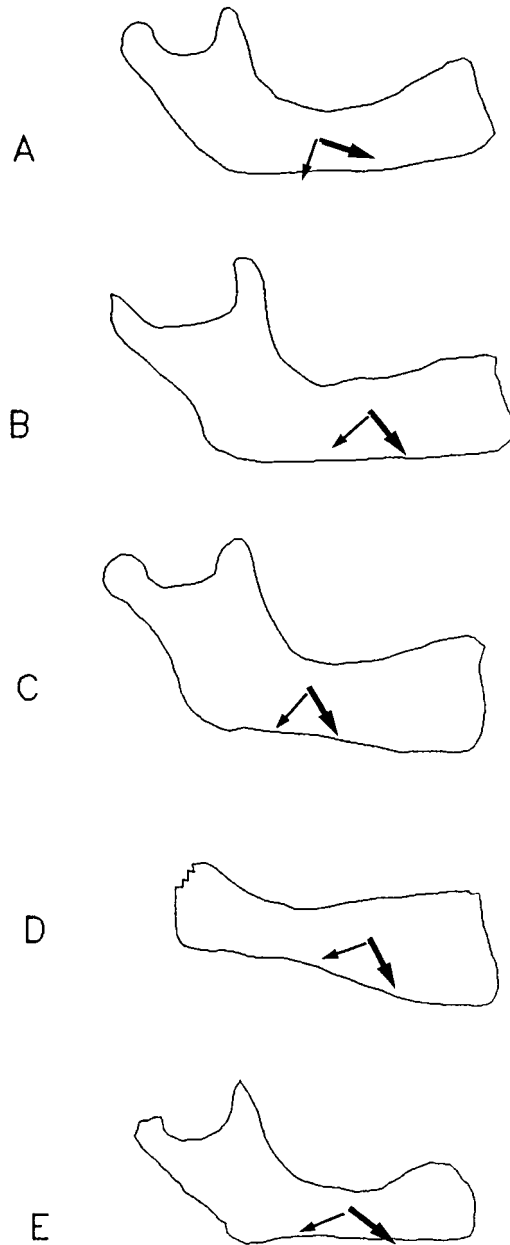


Fig. 3. Direction of the maximum principal strain (α) recorded from the midcorpus rosettes. Large arrows indicate α on the lateral surface, small arrows indicate α on the lingual surface. The orientation of α at approximately 45° to the corpus long axis and its reversal from lateral to medial surfaces are consistent with theoretical predictions for a twisted member.

³Recent unpublished work from one of our (DJD's) laboratories involved a similar experimental protocol to the one described in this study (see Fig. 2) using a dry, fully dentate *Macaca arctoides* mandible. The peak shear strains in torsion observed under the M_3 in this specimen reveal a profile similar to that observed in our human sample, with higher strains observed at midcorpus rosettes and a steeper strain gradient observed medially than laterally. The profile of strain from the macaque is most similar to that observed in specimen C in this study.

TABLE 2. Principal strain ratio at sampled sites

Specimen	Principal strain ratio (ϵ_1/ϵ_2)			
	MM	LM	MB	LB
A	0.80	1.48	0.92	0.49
B	1.00	1.50	0.86	0.78
C	0.89	1.08	1.52	0.30
D	1.03	0.89	0.83	1.25
E	1.04	1.75	0.76	0.60

Expected principal strain ratio = 1.0. Values given express the geometric mean of the principal strain ratio over 10 loading cycles. MM = medial midcorpus; LM = lateral midcorpus; MB = medial basal corpus; LB = lateral basal corpus.

are modelled as offset medially from the geometric center of the section (Biknevicius and Ruff, 1992), however, then the profile of the strain gradient makes more sense, since the cortical shell is consistently thinner medially than laterally within our sample. Thus, an asymmetrical ellipse model can account for this variation in cortical thickness.

Even so, given the morphology of the sampled specimens, this is not the only model which might have validity. A thin tube model of the corpus also appears to predict the site of largest shear strain, since there is an association between thin cortical bone and relatively high strains within experiments. The fact that the thinnest bone in our sample is always found along the medial aspect at midcorpus leaves us with two models which apparently work. The thin tube model makes no assumptions about cross-sectional shape, so the question arises as to whether a thin tube model is the model of choice. That is, given a corpus with very thin basal bone, would the ellipse model fail to predict the location of maximum strain? Our experiments suggest not, as midcorpus strains always exceed those along the basal aspect, even when the basal bone is as thin or thinner than that of the lateral midcorpus (e.g., experiments A through C, Fig. 1).

Bredt's formula provides a measure of strength in torsion that also considers cortical thickness variation in its calculation. Figure 5 compares the stress predicted at the location of the medial midcorpus rosette with the maximum shear strains recorded there in each specimen. What is evident from this plot is that this theoretical model bears a general, although certainly imperfect, resemblance to empirical observations. Bredt's formula, therefore, might serve as a useful model given the apparent role of cortical thickness in modulating strain magnitudes. Ideally, we could juxtapose these predicted stresses against similar values derived from an ellipse model. The problem with predicting absolute stresses using an ellipse model in this study is that sections including teeth and alveoli were sampled, such that the superior portion of sections could not be easily or consistently modelled. Comparing Bredt's formula with ellipse model prediction at sections between teeth (Biknevicius and Ruff, 1992), however, could document quantitatively discrepancies between these alternative models. Such results could, in turn, inform future experimental designs to test these models more precisely.

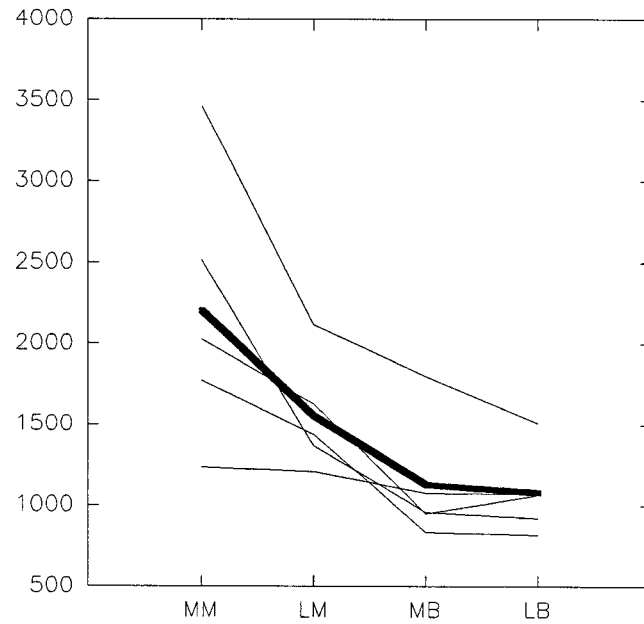
With these experiments, it is possible to reject the hypothesis that the mandible behaves as an open section. This model predicts the highest shear strains adjacent to the thickest region of cortical bone, and not one of our experiments is consistent with this model. Thus, one may infer that tooth roots and periodontal tissues, often neglected in comparative models, have a rigidifying or strengthening effect on the corpus such that its behavior is more similar to a closed section than to an open one (Daegling et al., 1992).

TABLE 3. Maximum shear stains under torsional loads

Experiment	Load (Nm)	Peak shear strain (SD)			
		MM	LM	MB	LB
A	5.53	2515 (25)	1368 (19)	960 (13)	922 (11)
B	5.28	1774 (15)	1436 (7)	835 (12)	818 (6)
C	5.65	1232 (51)	1207 (29)	1077 (25)	1067 (22)
D	5.47	2026 (20)	1628 (11)	949 (13)	1060 (6)
E	5.34	3467 (40)	2117 (26)	1801 (90)	1507 (10)

Peak shear units in microstrain. MM = medial midcorpus; LM = lateral midcorpus; MB = medial basal corpus; LB = lateral basal corpus. Mean peak shear strains and standard deviations are based on 10 loading cycles.

Fig. 4. Strain profiles for the five experiments with the superimposition of the mean profile (bold line). The Y-axis variable is peak shear strain (units in microstrain). The X-axis lists sites of strain sampling; the order of sites is arbitrary for the profile analysis. See text for explanation. MM = medial midcorpus rosette; LM = lateral midcorpus rosette; MB = medial basal rosette; LB = lateral basal rosette.



The remaining question is whether considerations of cross-sectional “shape” alone are informative as far as the inference of torsional strain gradients is concerned. If “robusticity” or “bending” indices reflect the general profile of strain gradient, then one should see smaller overall differences in peak surface strains within a section as an index approaches unity. The problem in evaluating this hypothesis from these experiments lies in subtle differences in strain gage placement among specimens (Fig. 1). Small differences in gage placement along the basal aspect must be influencing differences in the strain magnitudes recorded, with consequent impact on the profile of the observed strain gradient. It also must be recognized that we have not sampled the entire strain gradient in each specimen—

what we have done is estimate its general form from only four sites on the periosteal surface.

Figure 6 is a bivariate plot of the “bending” index for each specimen against the strain gradient observed on the lateral and medial corpora. In an attempt to account for gage placement differences, the gradient is here figured as $\Delta\gamma/d$, where d is the periosteal surface distance between the center of the midcorpus and basal gages on each side. For these experiments, the relationship between corpus “robusticity” and the profile of the strain gradient does not follow theoretical expectations along the medial corpus, and only generally follows expectations along the lateral corpus. This points out a flaw in the underlying rationale for using this index as a model for strain gradients (cf. Daegling and Grine, 1991; Schwartz and Conroy, 1996); specifically, the implicit assumption is that there is a symmetry of gradients between lateral and medial periosteal surfaces. Contour differences between these surfaces are obviously impacting the strain environment in a way that “shape” indices cannot discern.

This may not mean that specimen shape has no bearing on the profile of strain, but rather it suggests that shape and cortical thickness variation interact to determine

TABLE 4. Association of bone thickness and shear strain

Within specimens		By rosette location across specimens	
Specimen	r (Pvalue)	Location	r (Pvalue)
A	-0.983 (0.017)	Medial mid-corpus	-0.696 (0.192)
B	-0.436 (0.574)	Lateral mid-corpus	-0.203 (0.774)
C	-0.325 (0.675)	Medial basal	0.259 (0.674)
D	-0.955 (0.045)	Lateral basal	0.481 (0.412)
E	-0.941 (0.059)		

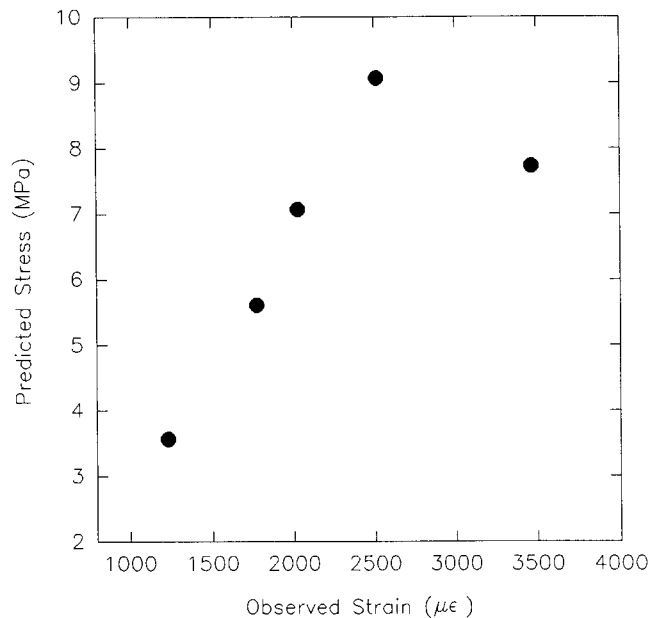


Fig. 5. Bivariate plot of stress predicted for each experiment by Bredt's formula vs. shear strain observed at the medial midcorpus rosette. A linear relationship would indicate good correspondence between theory and observation. The correlation between predicted stress and recorded strain is 0.77 ($P = 0.128$).

strain profiles. Thus, specimens with identical external contours cannot be expected to behave similarly unless the underlying cortical thickness is also the same.

Idealized models vs. real morphology

It is obvious that none of these models is structurally or materially reflective of "real" morphology. Actually what is at issue is whether these models can provide a consistent depiction of the strain environment. A variety of factors influencing strain magnitudes (bone density and anisotropy, structural complexity of the periodontium) are not considered in the models investigated here. The incorporation of these variables into finite element models is possible, although at present this has not been accomplished (Korioth et al., 1992; Hart et al., 1992; Chen, 1995). Whether these sophisticated modelling approaches can successfully deal with this problem is complicated by the fact that they remain cumbersome in construction and computation, and they do not account for population variation. It is certain that variation in density and material properties of mandibular bone within and between specimens must eventually be considered if fully quantitative models are to be developed (Dechow et al., 1992).

While the outcome of our experiments suggests that one may be cautiously optimistic about the use of relatively elementary structural models there remains the problem of modelling the behavior of the alveolar process, as the present study restricted its analysis to the mechanical behavior of the basal corpus. The reason for neglecting the alveolar process in this study was intentional because previous experimental work (Daegling and Hylander, 1994a,b) has indicated that the behavior of the alveolar process in torsion and bending does not conform satisfactorily to simple structural models of twisted and bent members. Obviously the interaction of teeth and periodontium modulates the distribution of surface strains, such that the biomechanical principles governing the behavior of the basal corpus do not apply equally to the alveolar process.

The fact that we may need two sets of models to understand the biomechanics of the corpus in some sense follows from the biology involved. As Moss (1968) has noted, the basal corpus and alveolar process perform fairly distinct functional roles, even though both regions must deal with the same sources of mechanical stress throughout life. The soft tissue environment or "functional matrix" (Moss, 1960, 1968) in

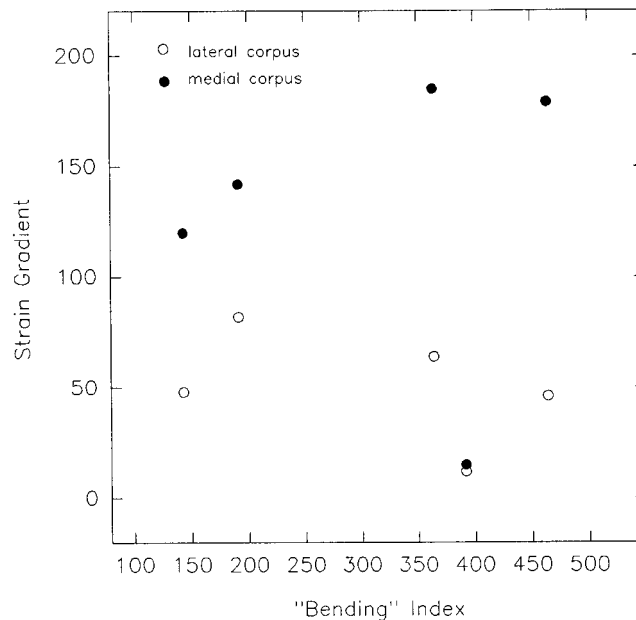


Fig. 6. Bivariate plot of the strain gradient observed in each experiment ($\Delta\gamma/d$, where d is the distance between midcorpus and basal rosettes on a given surface) vs. an index of specimen shape ($I_{\min}/I_{\max} \times 1000$). This "bending index" has been advocated by Daegling and Grine (1991) and Schwartz and Conroy (1996) on the premise that as the index increases the strain gradient decreases (an index of 1,000 would represent a cylindrical section). Medial and lateral strain gradients are shown. The proposed relationship is weak ($r = 0.04$ for medial gradients [$P = 0.995$]; $r = -0.45$ for lateral gradients [$P = 0.443$]). Variation in cortical thickness within sections is one factor that obscures the relationship between external geometry and strain gradients.

which each bony region develops is distinct, and there are different levels of osteogenic activity to distinguish these two regions as well (Reddy et al., 1991; Bouvier and Hylander, 1996). Furthermore, the fact that no one model is going to encompass the mechanics of the corpus is evident from structural considerations alone; i.e., the basal corpus is fairly homogeneous while the alveolar process is truly a composite structure.

An interesting development of these experiments is the perhaps unexpected departure of the principal strain ratio (ϵ_1/ϵ_2) from the "textbook" example of a twisted cylindrical rod. What to make of these departures is unclear. Theoretical discussions of principal strain proportions in twisted members of irregular geometry are nonexistent for a very good reason: engineers interested in designing structures that will sustain large twisting loads are not inclined to consider the behavior of bizarre shapes in their calculation of ideal solutions. One possible explanation is that bending is being superposed on the twisting load, although the lack of a consistent pattern (i.e., ratios always above or below 1.0 at a given rosette) does not support this possibility. It seems logical, however, to suppose that a "pure" twist will

not have identical effects throughout sections which lack axial or bilateral symmetry.

Another observation that requires comment concerns the relatively "diminished" strain gradient recorded in experiment C, which happened to be the only specimen with a complete dentition (see also footnote 3). This prompts the question of whether our results are an incidental effect of sampling partially edentulous individuals. Although we did not sample strains from areas that would have been prone to alveolar resorption, this process could influence strains in the basal corpus because of resulting changes in bone density and specimen geometry in resorptive areas. By sampling strains from beneath intact teeth, however, we have minimized these effects to some degree. In any case, dental status is certainly not the only explanation for the more equitable distribution of strains in this specimen given differences in overall shape and cortical bone distribution from the other specimens sampled. It is important to point out, moreover, that the observation of highest shear strains around midcorpus is consistent with the other experiments. The question of the influence of dental status on the precise form

of the strain gradient, however, remains open and is worth further investigation.

Is mandibular "robusticity" relevant for biomechanical inference?

The term "robust," when applied to descriptions of the mandible, has been used with different connotations. A robust mandible may be one that is relatively large and capable of sustaining heavy loads (Kelley and Pilbeam, 1986; Anapol and Lee, 1994), or it can refer to a mandible that is broad, relative to depth, in cross-sectional shape (Simons, 1964; Simons and Pilbeam, 1965; Frayer, 1974; Wood, 1976; Andrews, 1978). Many later Miocene and Pliocene hominoid mandibles can be described as "robust" because they fulfill both senses of the term. Unfortunately, there is sometimes unintended confusion created when the word is used interchangeably to refer to both biomechanical strength and geometrical shape (cf. Wolpoff, 1975; Chamberlain and Wood, 1985).

Despite this ambiguity, the index of corpus breadth over height is well-established in comparative studies, and the concept of "robusticity" as it refers to shape appears frequently in discussions of mandibular functional morphology (Jolly, 1970; Andrews, 1971; Wolpoff, 1975, 1977; Simons, 1977; Greenfield, 1979; Maw et al., 1979; Smith, 1983; Daegling and Grine, 1991; Schwartz and Conroy, 1996; Alpagut et al., 1996). Neither the "robusticity" index, as it is usually conceived, nor the "bending" index (Daegling and Grine, 1991; Schwartz and Conroy, 1996) can be used to infer differences in maximum strains between individuals or species. Furthermore, the experimental data presented here suggest that such indices do not yield useful information about the strain gradient within a section. The theoretical premise that a more "robust" (= cylindrical) mandible will exhibit a diminished strain gradient in torsion may only be true of restricted regions within a "robust" corpus. Corpus shape is but one factor governing the distribution of torsional strains; fortunately, by accounting for cortical thickness variation through use of an asymmetrical elliptical model, it should be possible to assess the

relative strains induced by torsion in mandibles of more or less similar design.

An important consideration ignored by the alternative models considered here is the problem created by irregularities in specimen geometry. Specifically, the presence of reentrant angles (i.e., sharply concave periosteal contours) is, at least theoretically, associated with stress concentrations (Young, 1989); concavities are often encountered along medial periosteal surfaces in the molar region in primate mandibles. Unfortunately, we cannot infer from experimental results whether stress concentrations occur in these regions since we could not sample strains at sites of maximum concavity, and also because stress and strain may not be linearly related under these conditions. Theoretical mathematical approaches may provide some guidance as to whether these concavities are associated with elevated stresses.

Implications for modern and fossil primates

It remains to be established whether the range of variation exhibited by primate mandibles is sufficiently restricted that a single structural model of the basal corpus can be meaningfully applied across the order. The hominoid postcanine mandibular corpus is sufficiently conservative in morphological variation such that an asymmetrical ellipse model could be productively applied. What constitutes a reliable model for the postcanine region in apes and humans, however, has no necessary bearing on the utility of that model for inferring states of stress and strain in other primates or in other regions of the corpus (i.e., in the vicinity of the mandibular symphysis).

Cross-sectional shape plays a role in governing strain gradients in the postcanine corpus, but this role becomes more ambiguous when the influence of other factors is considered. Though cross-sectional geometry appears to be an appropriate consideration for inference of strain gradients, it seems reasonable to suggest that consideration of "shape" alone will prove misleading. The results of our experiments suggest that variation in cortical bone thickness significantly influences strain gradients in torsion

to the point that the effects of specimen geometry may be partially obscured.

These observations bring forth an interesting problem with respect to "optimal" morphological solutions for dealing with the effects of torsion. Hylander (1979a, 1988) specifically related the unusual corpus morphology of *Paranthropus* to large torsional moments acting about the postcanine region in this genus. Corpus shape in *Australopithecus* and *Paranthropus* significantly departs from the condition in extant hominoids, while the details of cortical bone distribution within the corpus do not (Daegling and Grine, 1991). Theoretically, a redistribution of cortical bone more evenly throughout a section would provide an additional means by which to reduce maximum stresses and moderate strain gradients in torsion, yet for some reason these hominids (and other primates for which such data are available) do not employ this option. That is, medially thin cortical bone in the molar region appears to be stereotypical among higher primates (Daegling, 1990), which theoretically results in concentration of torsional strains in this region of the corpus. Whether this is really a suboptimal mechanical solution is unclear; it is equally plausible that our understanding of what constitutes an optimal stress environment is flawed.

A more thorough consideration of the in vivo context, however, may hold the answer. As Demes et al. (1984) hypothesized, when the effects of direct shear (imposed by occlusal force on the working-side corpus) are taken into account, the superposition of this source of stress on torsion places greater net stress on the lateral cortical plate and reduces net stress on the thinner medial compact bone. This explanation makes sense theoretically, although to date empirical corroboration is lacking.

The preceding comments underscore the important point that any interpretations arising from these results must be tempered by the understanding that torsion as a loading regime does not occur in isolation during mastication (Hylander, 1979b). Thus, we cannot relate the strain gradients observed in these experiments directly to the in vivo context. A complete accounting of the additional and simultaneous effects of bending

and direct shear on corpus strain might provide a clearer understanding of why cortical bone is distributed the way it is in primate jaws; however, even with a perfect understanding of loading conditions it is unrealistic to expect that bony morphology will reflect states of stress infallibly. Not only are there nonmechanical factors that influence the size and shape of the mandible (Smith, 1984; Dean and Beynon 1991), but there may also be safety factors related to trauma, in addition to those related to routine masticatory loads, that are implicated in the evolution of mandibular corpus morphology (Hylander and Johnson, in press).

CONCLUSIONS

On theoretical grounds it would appear to be inadvisable to infer states of stress and strain in the primate mandible via isotropic, homogeneous models that treat the jaw as a geometrically invariant body. Yet the results from experiments on human mandibles subjected to torsional loads suggest that modeling the basal corpus as an asymmetrical hollow ellipse may reliably reflect strain gradients in primate jaws. Both specimen shape and regional differences in bone thickness are factors conditioning the nature of the strain gradient.

For the particular loading regime of torsion of the postcanine corpus, the elementary models of mandibular form that have been widely employed in comparative research appear to be valid for comparison of relative strain magnitudes and the general characterization of where maximum strains occur below the alveolar process. That is, these models of the mandible as twisted members of uniform structure and material are probably capable of discerning meaningful biomechanical differences among primate species.

ACKNOWLEDGMENTS

Kirk Johnson is thanked for storage, retrieval, and analysis of the raw strain data. These data were originally presented in a symposium entitled "Biomechanics of Mammalian Feeding" at the 1996 Annual Meeting of the American Association of Physical Anthropologists. We wish to thank the organizers of that Symposium, Drs. C.E. Wall

and C.F. Ross, for inviting us to participate. We thank Dr. Emőke Szathmáry and three anonymous reviewers for their careful reading and thoughtful criticisms of previous drafts. Supported by the NSF (SBR-9307969) to DJD and WLH, NIH Merit Award (DE04531) to WLH, and NSF to DJD (SBR-9514213).

LITERATURE CITED

- Alpagut B, Andrews P, Fortelius M, Kappelman J, Temizsoy I, Celebi H and Lindsay W (1996) A new specimen of *Ankarapithecus meteai* from the Sinap formation of central Anatolia. *Nature* 382:349–351.
- Anapol F and Lee S (1994) Morphological adaptation to diet in platyrrhine primates. *Am. J. Phys. Anthropol.* 94:239–261.
- Andrews P (1971) *Ramapithecus wickeri* mandible from Fort Ternan, Kenya. *Nature* 231:192–194.
- Andrews PJ (1978) A revision of the Miocene Hominoida of East Africa. *Bull. Br. Mus. Nat. Hist.* 30:85–224.
- Biknevicius AR and Ruff CB (1992) Use of biplanar radiographs for estimating cross-sectional geometric properties of the mandible. *Anat. Rec.* 232:157–163.
- Bouvier M (1986a) A biomechanical analysis of mandibular scaling in Old World monkeys. *Am. J. Phys. Anthropol.* 69:473–482.
- Bouvier M (1986b) Biomechanical scaling of mandibular dimensions in New World monkeys. *Int. J. Primatol.* 7:551–567.
- Bouvier M and Hylander WL (1996) The mechanical or metabolic function of secondary osteonal bone in the monkey *Macaca fascicularis*. *Arch. Oral Biol.* 41:941–950.
- Chamberlain A and Wood BA (1985) A reappraisal of early hominid mandibular corpus dimensions. *Am. J. Phys. Anthropol.* 66:399–405.
- Chen X (1995) Biomechanics of the Hominoid Masticatory Apparatus. Ph.D. dissertation, Yale University.
- Cole TM (1992) Postnatal heterochrony of the masticatory apparatus in *Cebus apella* and *Cebus albifrons*. *J. Hum. Evol.* 23:253–282.
- Daegling DJ (1989) Biomechanics of cross-sectional size and shape in the hominoid mandibular corpus. *Am. J. Phys. Anthropol.* 80:91–106.
- Daegling DJ (1990) Geometry and Biomechanics of Hominoid Mandibles. Ph.D. dissertation, State University of New York at Stony Brook.
- Daegling DJ (1992) Mandibular morphology and diet in the genus *Cebus*. *Int. J. Primatol.* 13:545–570.
- Daegling DJ (1993) The relationship of in vivo bone strain to mandibular corpus morphology in *Macaca fascicularis*. *J. Hum. Evol.* 25:247–269.
- Daegling DJ and Grine FE (1991) Compact bone distribution and biomechanics of early hominid mandibles. *Am. J. Phys. Anthropol.* 86:321–339.
- Daegling DJ, and Hylander WL (1994a) Strain distribution in the human mandible. *Am. J. Phys. Anthropol. (Suppl.)* 18:75.
- Daegling DJ and Hylander WL (1994b) Profiles of strain in the human mandible. *J. Dent. Res.* 73 (Special Issue: IADR Abstracts):195.
- Daegling DJ, Ravosa MJ, Johnson KR and Hylander WL (1992) Influence of teeth, alveoli and periodontal ligaments on torsional rigidity in human mandibles. *Am. J. Phys. Anthropol.* 89:59–72.
- Dean MC and Beynon AD (1991) Tooth crown heights, tooth wear, sexual dimorphism and jaw growth in hominoids. *Z. Morphol. Anthropol.* 78:425–440.
- Dechow PC, Schwartz-Dabney CL and Ashman R (1992) Elastic properties of the human mandibular corpus. In SA Goldstein and DS Carlson (eds.): *Bone Biodynamics in Orthodontic and Orthopedic Treatment*, Volume 27, Craniofacial Growth Series. Ann Arbor: Center for Human Growth and Development, University of Michigan, pp. 299–314.
- Demes B, Preuschoft H and Wolff JEA (1984) Stress-strength relationships in the mandibles of hominoids. In DJ Chivers, BA Wood, and A Bilsborough (eds.): *Food Acquisition and Processing in Primates*. New York, Plenum, pp. 369–390.
- Frankel VH and Burstein AH (1965) Load capacity of tubular bone. In RM Kenedi (ed.): *Biomechanics and Related Engineering Topics*. Oxford, Pergamon, pp. 381–396.
- Frankel VH and Burstein AH (1970) *Orthopaedic Biomechanics*. Philadelphia: Lea and Febiger.
- Frazer DW (1974) A reappraisal of *Ramapithecus*. *Yrbk. Phys. Anthropol.* 18:19–30.
- Greenfield LO (1979) On the adaptive pattern of "Ramapithecus." *Am. J. Phys. Anthropol.* 50:527–548.
- Hart RT, Hennebel VV, Thongpreda N, Van Buskirk WC and Anderson RC (1992) Modeling the biomechanics of the human mandible: A three-dimensional finite element study. *J. Biomech.* 25:261–286.
- Hylander WL (1979a) Mandibular function in *Galago crassicaudatus* and *Macaca fascicularis*: An in vivo approach to stress analysis of the mandible. *J. Morphol.* 159:253–296.
- Hylander WL (1979b) The functional significance of primate mandibular form. *J. Morphol.* 160:223–240.
- Hylander WL (1981) Patterns of stress and strain in the macaque mandible. In DS Carlson (ed.): *Craniofacial Biology*. Monograph 10, Craniofacial Growth Series. Ann Arbor: Center for Human Growth and Development, University of Michigan, pp. 1–37.
- Hylander WL (1984) Stress and strain in the mandibular symphysis of primates: A test of competing hypotheses. *Am. J. Phys. Anthropol.* 64:1–46.
- Hylander WL (1985) Mandibular function and biomechanical stress and scaling. *Am. Zool.* 25:315–330.
- Hylander WL (1988) Implications of in vivo experiments for interpreting the functional significance of "robust" australopithecine jaws. In FE Grine (ed.): *Evolutionary History of the Robust Australopithecines*. New York: Aldine de Gruyter, pp. 55–83.
- Hylander WL and Johnson KR (in press) Functional Morphology and in vivo bone strain patterns in the craniofacial region of primates. In JM Plavcan, RF Kay and K van Schaik (eds.): *Reconstructing Behavior in the Primate Fossil Record*. New York: Plenum.
- Jolly CJ (1970) The seed-eaters: A new model of hominid differentiation based on a baboon analogy. *Man* 5:5–26.
- Kelley J and Pilbeam DR (1986) The dryopithecines: Taxonomy, comparative anatomy and phylogeny of Miocene large hominoids. In DR Swindler and J Erwin (eds.): *Comparative Primate Biology*, Volume I: Systematics, Evolution and Anatomy. New York: Alan R. Liss, pp. 361–412.
- Korioth TWP, Romilly DP and Hannam AG (1992) Three-dimensional finite element stress analysis of the dentate human mandible. *Am. J. Phys. Anthropol.* 88:69–96.
- Maw B, Ciochon RL and Savage DE (1979) Late Eocene of Burma yields earliest anthropoid primate, *Pondaungia cotteri*. *Nature* 282:65–67.
- Moss ML (1960) A functional analysis of human mandibular growth. *Am. J. Prosth. Dent.* 10:1149–1160.

- Moss ML (1968) Functional cranial analysis of mammalian mandibular ramal morphology. *Acta Anat.* 71:423–447.
- Nash WA (1972) *Strength of Materials*. 2nd ed. New York: McGraw-Hill.
- Ravosa MJ (1991) Structural allometry of the prosimian mandibular corpus and symphysis. *J. Hum. Evol.* 20:3–20.
- Reddy MS, English R, Jeffcoat MK, Tumeh SS and Williams RC (1991) Detection of periodontal disease activity with a scintillation camera. *J. Dent. Res.* 70:50–54.
- Rencher AC (1995) *Methods of Multivariate Analysis*. New York: John Wiley and Sons.
- Schwartz GT and Conroy GC (1996) Cross-sectional geometric properties of the *Otavipithecus* mandible. *Am. J. Phys. Anthropol.* 99:613–623.
- Simons EL (1964) On the mandible of *Ramapithecus*. *Proc. Natl. Acad. Sci. U.S.A.* 51:528–535.
- Simons EL (1977) *Ramapithecus*. *Sci. Am.* 236:28–35.
- Simons EL and Pilbeam DR (1965) Preliminary revision of the Dryopithecinae (Pongidae, Anthroidea). *Folia Primatol.* 3:81–152.
- Smith RJ (1983) The mandibular corpus of female primates: taxonomic, dietary, and allometric correlates of interspecific variations in size and shape. *Am. J. Phys. Anthropol.* 61:315–330.
- Smith RJ (1984) Comparative functional morphology of maximum mandibular opening (gape) in primates. In DJ Chivers, BA Wood and A Bilsborough (eds.): *Food Acquisition and Processing in Primates*. New York: Plenum, pp. 231–255.
- Wilkinson L (1990) *SYSTAT: The System for Statistics*. Evanston, IL: Systat Inc.
- Wolpoff MH (1975) Some aspects of human mandibular evolution. In JA McNamara Jr. (ed.): *Determinants of Mandibular Form and Growth*. Craniofacial Growth Series Monograph 4. Ann Arbor: Center for Human Growth and Development, University of Michigan, pp. 1–64.
- Wolpoff MH (1977) Systematic variation in early hominid corpus dimensions. *Anthropol. Anz.* 36:3–6.
- Wood BA (1976) Remains attributable to *Homo* in the East Rudolf succession. In Y Coppens, F Clark-Howell, GL Isaac and REF Leakey (eds.): *Earliest Man and Environments in the Lake Rudolf Basin: Stratigraphy, Paleoecology and Evolution*. Chicago, University of Chicago Press, pp. 490–506.
- Young WC (1989) *Roark's Formulas for Stress and Strain*. 6th ed. New York: McGraw-Hill.